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A Pliosaurid Plesiosaurian from the Rosso Ammonitico Veronese Formation of Italy

Authors: Cau, Andrea, and Fanti, Federico

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ANDREA CAU and FEDERICO FANTI

Plesiosauria is a clade of medium to large bodied marine reptiles with a cosmopolitan distribution ranging from the latest Triassic to the end of the Cretaceous. In Europe, the fossil record of Plesiosauria is mainly known from the Northern latitudes, whereas it is much rarer from the Southern and Mediterranean areas. Here, we report the first articulated skeleton of an Italian plesiosaurian, from the Callovian–Oxfordian deposits of the Rosso Ammonitico Veronese Formation of Kaberlaba (Veneto). The specimen is referred to Pliosauridae based on the large size of the skull, compared to the appendicular skeleton, the presence of the lacrimal, and a distinct anterolateral projection of the prefrontal into the orbital margin. Mandibular and vertebral symplesiomorphies support the placement of the Italian taxon among the "gracile-longirostrine grade" of basal pliosaurids. The Kaberlaba plesiosaurian represents the second reptile clade recovered from the Rosso Ammonitico Veronese Formation, after Thalattosuchia.

Key words: Reptilia, Plesiosauria, palaeobiogeography, Rosso Ammonitico Veronese Formation, Callovian–Oxfordian, Italy.

Andrea Cau [cauand@gmail.com], Museo Geologico e Paleontologico "Giovanni Capellini", Alma Mater Studiorum, Università di Bologna, via Zamboni 63, 40126 Bologna, Italy;
Federico Fanti [federico.fanti@unibo.it], Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum, Università di Bologna, via Zamboni 67, 40126 Bologna, Italy.

Introduction

Plesiosaurians were obligate aquatic sauropterygian diapsids with a cosmopolitan distribution spanning from the latest Triassic to the end of the Cretaceous. The first plesiosaurians were discovered 200 years ago in Jurassic formations of Northern Europe (Evans 2010), a region that has since been among the most prolific in term of both plesiosaurian diversity and disparity (Andrews 1910; Tarlo 1960; Ketchum and Benson 2010 and reference therein). Compared to their Northern counterparts, plesiosaurians from Southern Europe are rarer and often represented by fragmentary remains (e.g., Smith et al. 2012). As a consequence, few South European plesiosaurians have been included in large phylogenies of Plesiosauria, nor have they been discussed in detail in terms of the macroevolution of the group (Bardet et al. 1999; O'Keefe 2001, 2004; Gasparini 2009; Ketchum and Benson 2010, 2011a; Benson et al. 2012). The fossil record of plesiosaurians from Italy has so far consisted only of isolated bones with poorly diagnostic features (Renesto 1993; Dalla Vecchia et al. 2005). This is noteworthy, given the relative abundance of Triassic basal (non-plesiosaurian) sauropterygians from this region (Rieppel 2000; Dalla Vecchia 2006).

In this study, we describe the first articulated skeleton of a plesiosaurian from Italy, and one of the few found in the Jurassic of Southern Europe. The specimen was collected in the 1980s from an active quarry at the Kaberlaba locality near Asiago (Veneto, North-Eastern Italy). All preserved elements were removed from a nodular and cherty interval of the exposed Middle Unit of the Rosso Ammonitico Veronese Formation (Middle–Upper Jurassic; sensu Martire et al. 2006) and consequently moved to the Museo Paleontologico e della Preistoria "Pietro Leonardi" in Ferrara.

Institutional abbreviations.—MPPL, Museo Paleontologico e della Preistoria "Pietro Leonardi", Ferrara, Italy.

Other abbreviations.—LRAV, Lower Rosso Ammonitico Veronese; MRAV, Middle Rosso Ammonitico Veronese; RAV, Rosso Ammonitico Veronese; URAV, Upper Rosso Ammonitico Veronese.
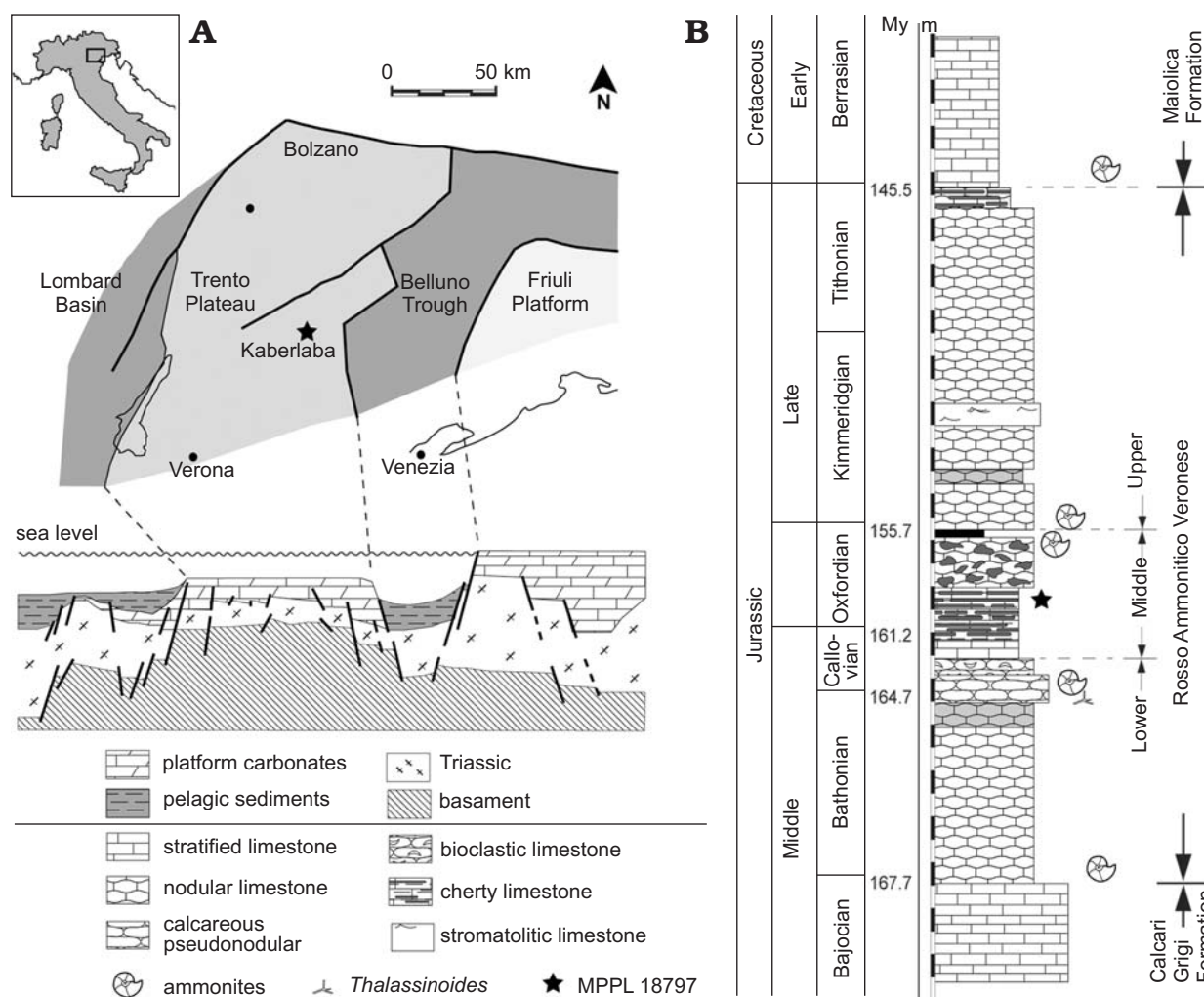
Fig. 1. **A**. Geographic location of the Kaberlaba section in north-eastern Italy and Middle Jurassic palaeogeographic realms with simplified cross-section of part of the South Alpine margin. **B**. Stratigraphic section of the Kaberlaba quarry in the Altopiano di Asiago (Vicenza) (modified after Martire et al. 2006).

Geological setting

During the Middle and early Late Jurassic, the Southern Alps of Italy comprised four major structural and palaeogeographic areas (Fig. 1A): from west to east, the Lombardo Basin, the Trento Plateau, the Belluno trough, and the Friuli Platform (Martire et al. 2006). Palaeogeographic reconstructions locate the Asiago area near the eastern margin of the Trento Plateau during the Middle–early Late Jurassic (Thierry 2000). The Rosso Ammonitico Veronese Formation (Bajocian–Tithonian) is a typical lithostratigraphic unit within the Mesozoic successions of the Trento Plateau and consists primarily of red, ammonite-bearing, nodular limestone (Ferrari 1982; Clari et al. 1990; Sarti 1993; Martire 1996; Martire et al. 2006; Chiari et al. 2007; Großmann 2007). The RAV is subdivided into three units: in ascending order, Lower Rosso Ammonitico Veronese (upper Bajocian–lower Callovian), Middle Rosso Ammonitico Veronese (upper Callovian–middle Oxfordian), and Upper Rosso Ammonitico Veronese (lower Kimmeridgian–Tithonian). Relevant to this study, the

Kaberlaba section of Martire et al. (2006) has been proposed as type section for the RAV Formation, having a complete record of its three members. The fossil reptile described herein was collected from the upper cherty deposits of the MRAV (Lithozone 5 of Martire et al. 2006; Fig. 1B), which ranges in age from the uppermost Callovian to the middle Oxfordian. This interval is characterized by the abundance of nodules and lenses of red chert, resulting in an irregular bedding style. Limestone rocks are wackestones to packstones with common radiolarians and sponge spicules and minor thin-shelled bivalves. The lower deposits of this unit are devoid of significant fossils, whereas a middle Oxfordian ammonite fauna characterizes the main body of the MRAV (Martire 1996; Martire et al. 2006).

Nodular beds at the top of the LRAV as well as recurrent cherty beds within the MRAV document that the Kaberlaba section is a more complete succession than in other parts of the Trento Plateau (where the MRAV is not preserved) and also suggests a deeper part of the basin. The relative articulation of preserved elements in the fossil indicates that the carcass suffered minimal to moderate disturbance and was
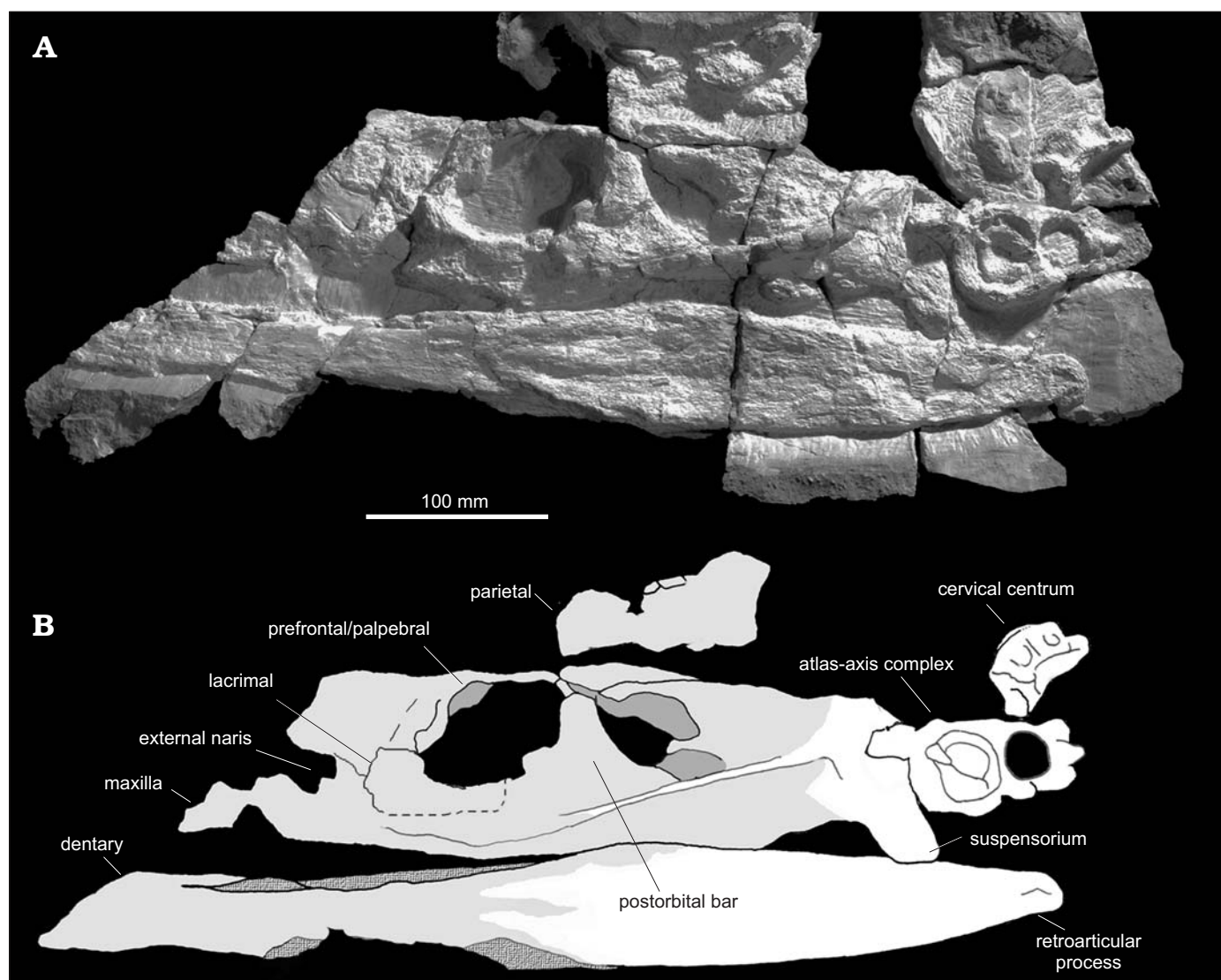
Fig. 2. Partial skull and anterior cervical vertebrae of unidentified pliosaurid plesiosaurian (MPPL 18797) from the uppermost Callovian–middle Oxfordian of Kaberlaba (Asiago, Italy), in left lateral view. Photograph (**A**) and explanatory drawing (**B**). White, preserved bone surfaces; dark grey, preserved margins of skull fenestrae; light grey, eroded bone surface; cross hatching, broken bone.

buried in a low-energy environment. Besides the plesiosaurian bones, the other fossil remain found in the quarry were small and isolated shark teeth, possibly belonging to scavengers of the carcass.

Although known for more than two centuries, the rare reptilian fossils from the RAV Formation have received little attention, mainly due to their fragmentary condition (Cau and Fanti 2011, and reference therein). The first named reptile species from the RAV Formation was "*Steneosaurus barettoni*" (Omboni 1890), a thalattosuchian crocodyliform based on a partial skull and mandible that requires detailed redescription (AC unpublished material). The second reptile species was the geosaurine metriorhynchid *Neptunidraco ammoniticus*, from the Bajocian–Bathonian of the LRAV (Cau and Fanti 2011). The pliosaurid MPPL 18797 thus represents the second reptilian clade recovered from the RAV Formation, after Thalattosuchia.

Systematic palaeontology

Plesiosauria de Blainville, 1835

Pliosauridae Seeley, 1874

Genus et species indet.

Figs. 2–6 (for measurements of bones, see SOM: Supplementary Online Material available at http://app.pan.pl/SOM/app59-Cau_Fanti_SOM.pdf).

Material.—MPPL 18797: partial skull and mandible; 32 isolated teeth; cervical, dorsal and caudal vertebrae; right scapulocoracoid; femur, two epipodials and isolated metapodial elements; additional broken undetermined fragments from Kaberlaba quarry, Asiago Municipality, Vicenza Province, Italy (Fig. 1A). Uppermost Callovian–middle Oxfordian. Lithozone 5, Middle Unit, Rosso Ammonitico Veronese Formation (Martire et al. 2006; Fig. 1).

Description

MPPL 18797 includes more than 75 bone and tooth elements, from the same individual (see SOM). The skull, mandible, pectoral region and preserved tail elements show little or moderate disarticulation. Although most bones appear little distorted or deformed, the sutures along adjacent bones are hardly discernible.

Skull and dentition.—Most of the preorbital part of the skull and the anterior end of the mandible were not recovered. The skull roof is almost completely lost, with only a fragment of the parietal preserved (Fig. 2). The lateral surfaces of the orbital and temporal bones are mediolaterally compressed and the bone boundaries and articulations are poorly distinguishable. The maxillary fragment lacks most of the oral margin, and its lateral surface is mostly eroded. The posteroventral corner of the external naris is preserved as a small cleft along the dorsal margin of the maxilla, placed about 40 mm anteriorly to the orbital margin. The latter is roughly elliptical, with the long axis oriented posterodorsally relative to the skull anteroposterior axis. It is slightly constricted at the anterodorsal and posteroventral corners, and is marked by margins distinctly raised dorsolaterally. The anterodorsal constriction of the orbit is interpreted as being produced by the anterolateral projection of the prefrontal (e.g., Gasparini 2009). Alternatively, it may represent a palpebral (Ketchum and Benson 2011b). The lacrimal forms the anteroventral margin of the orbit, excluding the maxilla from the latter, and articulates with the anteroventral margin of the prefrontal, as in other pliosaurids (Ketchum and Benson 2011b). The postorbital bar is trapezoidal and expanded anteroventrally. The lateroventral margin of the temporal fenestra is only partially preserved and appears roughly semicircular. The temporal region is about 130% longer than the orbit. From the preserved parietal it is possible to conclude that the dorsal margin of the skull is posterodorsally directed above the orbit, possibly indicating the presence of a raised parietal crest. The suspensorium is robust laterally and projects slightly posteroventrally. The mandible is gracile, with the minimum height of the dentary no more than 8% of the preserved length of the mandible. The dentary is straight, with dorsal and ventral margins almost parallel, where preserved. The mandibular glenoid is poorly exposed in lateral view, suggesting it was directed dorsomedially. If present, the coronoid was not exposed laterally. There is no evidence of a foramen between the lateral surfaces of surangular and angular. The shape and extent of the sutural contact along the latter two bones is unclear. Several teeth, ranging between 6 and 12 mm in crown apicobasal length, are preserved near the skull, although none in its alveolus. Teeth are suboval in cross section, with slight labiolingual compression (Fig. 3A); the crowns are distolingually recurved and bear a series of slightly developed enamel ridges that are apicobasally oriented. The best preserved teeth show a slight ridge running along the apicobasal axis at the centre of the convex surface, whereas the apicobasally concave (lingual) surface lacks a distinct ridge (Fig. 3A).
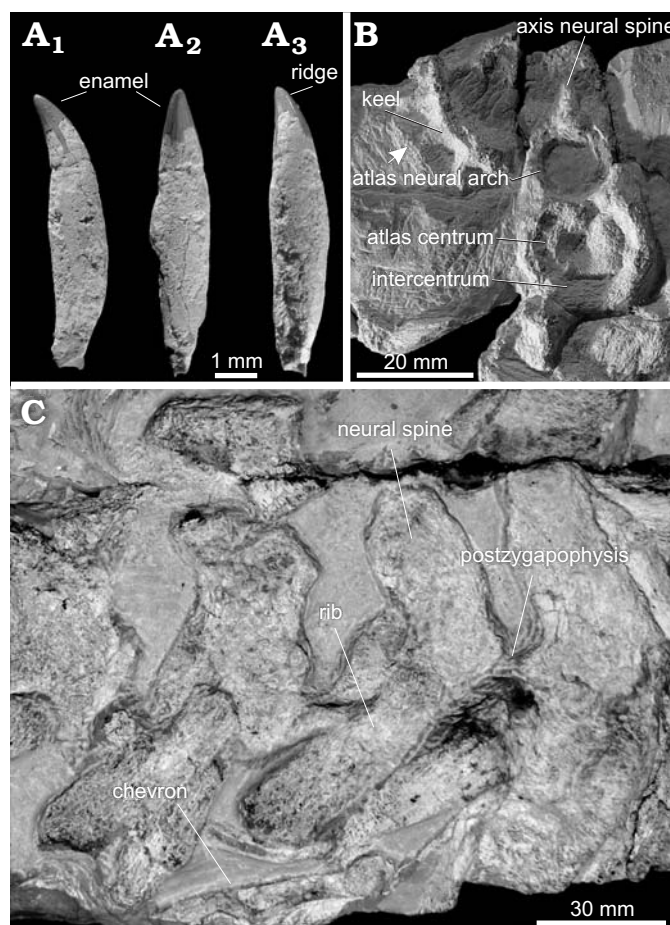

Fig. 3. Unidentified pliosaurid plesiosaurian (MPPL 18797) from the uppermost Callovian–middle Oxfordian of Kaberlaba (Asiago, Italy). **A**. Isolated tooth in lingual (A_1), distal (A_2), and mesial (A_3) views. **B**. Detail of the atlas-axis complex (anterior view) and an anterior postaxial cervical vertebra (arrow, ventral view). **C**. Detail of articulated caudal vertebrae in right lateral view.

Vertebrae and ribs.—No more than ten presacral vertebrae are preserved. Therefore, direct estimation of neck and trunk length is not possible. The atlas-axis complex, exposed in anterior view (Fig. 3B), is similar to *Marmornectes* (Ketchum and Benson 2011a: fig. 6). The axial neural spine is low and mediolaterally compressed (Fig. 3B). The isolated anterior cervical centra are shortened, being wider than long (Figs. 2, 3B). The cervical centra show a convex ventral margin of the articular facets. A low, rounded keel runs along the ventral surface of the cervical centra, delimiting medially two shallow fossae housing the subcentral foramina. The articular surface of the anteriormost cervical centra is flattened, wider than tall. The preserved four dorsal centra are semi-articulated and pressed up against the coracoid (Fig. 4). The dorsal centra are about as long as wide (see SOM), with a gently rounded ventral surface. A semi-articulated series of about 12 proximal caudal vertebrae is preserved (Figs. 3C, 5). Other caudal vertebrae, from the proximal region of the tail, are associated with hind limb elements (Fig. 6). The caudal centra are amphicoelous, taller and wider than long. The
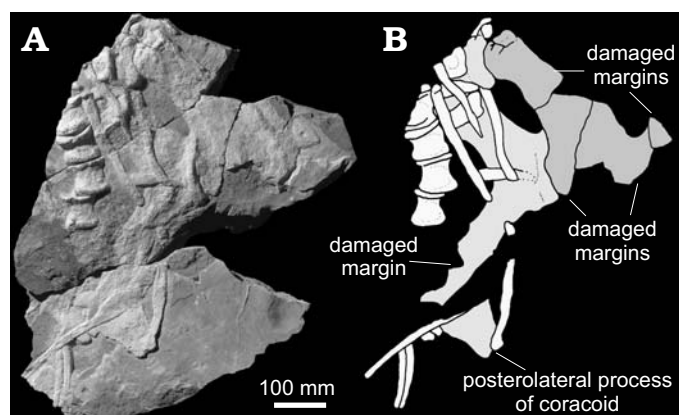
Fig. 4. Semi-articulated dorsal vertebrae, ribs and right scapulocoracoid (anterior end above) of the unidentified pliosaurid plesiosaurian (MPPL 18797) from the uppermost Callovian–middle Oxfordian of Kaberlaba (Asiago, Italy). Photograph (**A**) and explanatory drawing (**B**). White, preserved bone surfaces; dark grey, scapula; light grey, coracoid; white, vertebrae and ribs.
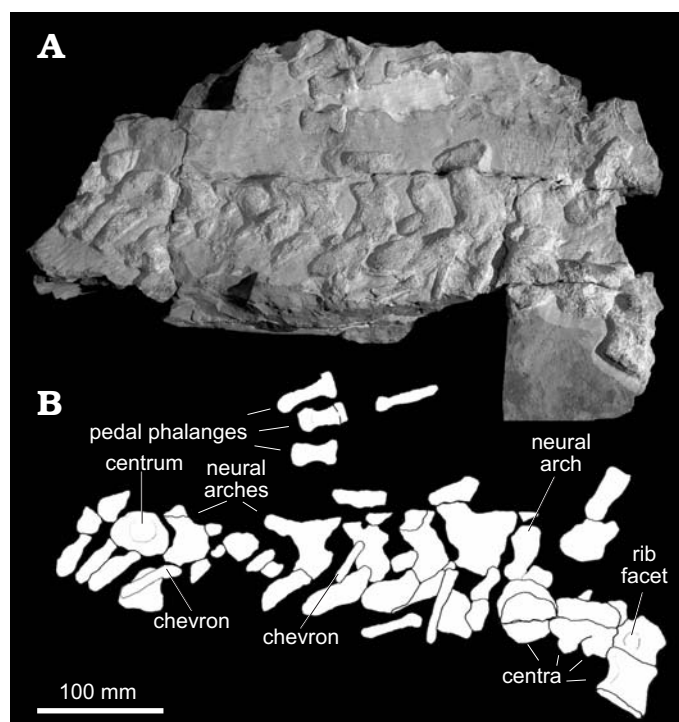

Fig. 5. Semi-articulated caudal vertebral series (anterior end to the right) and isolated pedal phalanges of the unidentified pliosaurid plesiosaurian (MPPL 18797) from the uppermost Callovian–middle Oxfordian of Kaberlaba (Asiago, Italy). Photograph (**A**) and explanatory drawing (**B**).

preserved rib facets are placed almost entirely on the centra. Most of the neural arches are crushed. When preserved, the caudal neural arches bear well-developed zygapophyses and posterodorsally directed neural spines (Fig. 3C). Several ribs are preserved in close association with the caudal vertebrae (Fig. 3C). The caudal ribs are elongate, mediolaterally compressed, with a rounded proximal end, a slightly constricted "neck" and a distal "paddle-like" end. The preserved chevrons are slender straight rods (Fig. 3C).

Appendicular skeleton.—The right scapulocoracoid is badly preserved and prominently compressed dorsoventrally. The scapula is about twice as long as its posterior width (Fig. 4). The scapula seems to contact the anteromedial process of the coracoid, as in plesiosauroids (Storrs 1997; Grossmann 2007; Ketchum and Benson 2010; Smith and Vincent 2010), although it may be a preservational artefact. Posterodistally, the scapula is incompletely preserved. The coracoid is longer than the scapula, as in most plesiosaurians (O'Keefe 2002; Ketchum and Benson 2010). The preglenoid process is well developed (Cruickshank 1994; Ketchum and Benson 2011a)*,* although the exact shape cannot be determined due to breakage and coverage by other bones. The posterolateral process of the coracoid is a large trapezoid pointing laterally. Although deformed by compression, a propodial, interpreted as a femur (see Benson et al. 2011: fig. 15) appears as paddle-shaped, and poorly expanded distally (Fig. 6). Bone fragments tightly appressed to the femur are interpreted as remains of the pelvic bones (Fig. 6). Badly preserved epipodials are placed distally to the femur. Some isolated pedal phalanges are preserved near the caudal vertebrae (Fig. 5): phalanges are about twice as long as proximally wide and constricted at mid-length.

Discussion

MPPL 18797 is referred to Plesiosauria based on the presence of subcentral foramina in the cervical vertebrae, absence of cervical zygosphenes, and presence of a relatively large coracoid (Ketchum and Benson 2010). In the absence of a complete skeleton, a comparison between the preserved skull size (>520 mm long) and the appendicular bones in MPPL 18797 was used to infer its position along the "plesiosauromorph-pliosauromorph" continuum of body proportions (O'Keefe 2002). This specimen had a skull longer than any known Jurassic plesiosauroid of comparable appendicular size, and similar in length to pliosauromorph taxa. Albeit incomplete, the preserved skull in MPPL 18797 is about 150% longer than the complete skulls in non-polycotylid plesiosauroids of comparable appendicular size (e.g., *Hydrotherosaurus*; O'Keefe 2002) and indicates an animal with a skull length to femur length ratio >1.25, and thus a minimum total skull to femur length ratio in the upper range of, or higher than, those among all non-polycotylid Plesiosauroidea (e.g., the same ratio in *Cryptoclidus*, 0.89–1.05; *Hydrotherosaurus*, 0.92; *Plesiosaurus dolichodeirus*, 0.93–1.00; Storrs 1997; O'Keefe 2002), and comparable to or even higher than the values in non-plesiosauroid plesiosaurians like *Attenborosaurus*, 1.32 and *Hauffiosaurus*, 1.25 (O'Keefe 2002). The same ratio is comparable or higher in some polycotylids (*Polycotylus*, 1.32), and extreme in other polycotylids like *Dolichorhynchops*, 2.04, and in more derived pliosauroids like *Peloneustes*, 1.57 and *Liopleurodon*, 1.73 (O'Keefe 2002). We thus conclude that the skull of MPPL 18797 was at least as elongate as in basal pliosaurids and some polycotylid. According to O'Keefe (2002), in
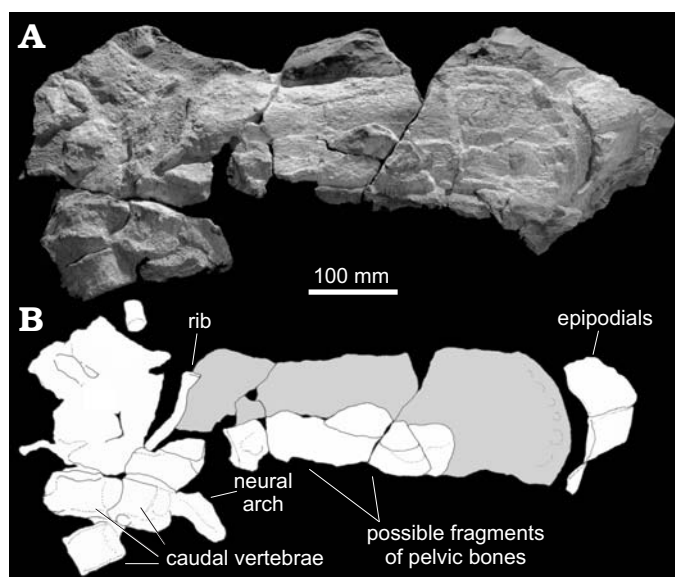
Fig. 6. Caudal vertebrae and hindlimb elements of the unidentified pliosaurid plesiosaurian (MPPL 18797) from the uppermost Callovian–middle Oxfordian of Kaberlaba (Asiago, Italy). Photograph (**A**) and explanatory drawing (**B**). Grey tones indicate the femur.

plesiosaurian evolution the neck elongation and skull elongation usually show opposite trends. Given the relationships between body proportion, skull and neck elongations in Plesiosauria (with long-skulled forms showing relatively shorter necks and deeper bodies; Massare 1988; O'Keefe 2002), the inferred longer skull in MPPL 18797 suggests that its neck was relatively shorter and the body relatively deeper than in Jurassic plesiosauroids, and comparable to pliosaurids and polycotylids. Therefore, although a precise quantification of its proportions is impossible, we hypothesise the body shape of the Italian plesiosaurian as more "pliosauromorph" than in Jurassic plesiosauroids, supporting a referral to Pliosauridae. This interpretation is further supported by the presence of the lacrimal and an anterolateral projection of the prefrontal (perhaps a distinct palpebral ossification, see Ketchum and Benson 2011b), forming the orbital margin and embaying the orbit, as in derived pliosaurids (e.g., Gasparini 2009; Ketchum and Benson 2010, 2011b). The combination of shallow and elongate proportions of the mandible, and dorsomedially inclined mandibular glenoid support the placement of MPPL 18797 among the "gracile longirostrine-grade" of Pliosauridae (Ketchum and Benson 2011a).

The enamel ornamentation of the rostralmost dentition is diagnostic at the genus and species level among Jurassic pliosaurids, whereas the morphology of the posteriormost teeth is more conservative and has poor taxonomic value (Tarlo 1960; Gasparini 1997; Ketchum and Benson 2011a). All the teeth are interpreted as belonging to the posterior end of the tooth-row, and thus do not permit identification to a particular genus or species of pliosaurid. Based on tooth crowns with sub-oval cross section, we dismiss referral of the Italian pliosaurid to *Pliosaurus* or *Gaillardosaurus* (Tarlo 1960; Massare 1988; Gasparini 2009). Although in overall morphology, the Italian

pliosaurid is similar to *Peloneustes*, its only autapomorphy (Ketchum and Benson 2011b: 642) cannot be determined in MPPL 18797. Furthermore, the narrow axial neural spine in the Kaberlaba plesiosaurian, differing from the broader spine in *Hauffiosaurus* and *Liopleurodon*, may indicate that it was more basal among Pliosauridae (Benson et al. 2011, 2012).

Comparison with well-preserved plesiosaurian skeletons (Newman and Tarlo 1967; Brown 1981; Storrs 1997; Smith and Vincent 2010; Benson et al. 2011) indicates an estimated body length of MPPL 18797 of about 3–4 m. The moderately expanded orbits facing laterally, the gracile and relatively elongate mandible and the small, slender, and slightly curved teeth with fine ornamentation suggest that the Italian pliosaurid was a predator of soft or small-bodied prey in euphotic epipelagic environment (Massare 1988, 1997).

During the Callovian–Oxfordian, the Trento Plateau and the Kaberlaba locality were located within the Tethyan domain and separated from the European landmasses by a deep oceanic basin (Clari et al. 1990; Sarti 1993; Martire 1996; Martire et al. 2006). Recent discoveries in Central and South America of vertebrate taxa with Western Tethyan and North European affinities (pleurodiran turtles, plesiosauroids, pliosauroids, ophthalmosaurid ichthyosaurs, and metriorhynchoids; Gasparini and Fernández 1997; Fernández and Iturralde-Vinent 2000; De la Fuente and Iturralde-Vinent 2001; Shultz et al. 2003; Gasparini 2009) support the presence of a marine seaway connecting the western Tethys with the Pacific and Boreal Realms during the Oxfordian. Notably, two distinct latitudinal belts characterize the European platform and the Mediterranean Tethys during the Late Jurassic (Cecca et al. 2005 and reference therein). In particular, well-constrained palaeobiogeographic patterns of coral reefs, cephalopods, ostracodes, and neoselachians, as well as inferred climatic oscillation from oxygen isotopes, support a northern Boreal domain over the European platform, and a southern Tethyan domain (Stevens 1963; Hallam 1969; Dommergues 1987; Doyle 1987; Westermann 2000; Kriwet and Klug 2008). These two domains are believed to reflect major climatic, salinity, and depositional variations (Hallam 1969; Doyle 1987). Shallow, epicontinental areas in the southern European platform are believed to represent the possible "mixing zone" of such domains. Relevant to this study, the hypothesized southern limit of "Boreal" influence for the Oxfordian is located about 500 km north of the Trento Plateau area, thus supporting "true" Tethyan conditions in the Kaberlaba locality (Clari et al. 1990; Kriwet and Klug 2008). Although badly preserved, MPPL 18797 is significant as the first plesiosaurian skeleton based on articulated remains recovered from Italy, and one of the few from Southern Europe.

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